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XXXVI.—*Notes on* Prof. Steenstrup's *Views on the Obliquity of Flounders**. By Prof. Wyville Thomson, LL.D., F.R.S.E., M.R.I.A., F.G.S.

[Plate XVIII.]

Any contribution from the pen of the accomplished author of the 'Alternation of Generations' must be welcome; and the present communication "On the Migration of the upper Eye of Flounders, across, through the Head, from the blind side to the eye-side," almost vies in novelty with the author's earlier memoir. The original paper is in Danish, and consequently a sealed book to most English students; and many interesting points are omitted in Prof. Steenstrup's French letter to M. Milne-Edwards. We shall therefore commence with a tolerably full abstract of the communication to the Danish Academy, reserving any remarks we may have to offer until the reader is in full possession of the author's views.

I.

The general fact of the obliquity of the Pleuronectidæ is well known. All Flounders have a high compressed body, whose two sides are unequally developed. This want of symmetry is universally accompanied by another peculiarity: both eyes are brought round to one side of the head, so that the fish acquires an eye side and a blind side. The former is coloured and turned upwards towards the light; the latter is colourless or white, and turned downwards in motion or rest. The fish moves or lies

* J. Japetus Sm. Steenstrup:—'Om Skjaevheden hos Flynderne, og navnlig om Vandringen af det övre Öie fra Blindsiden til Öiesiden tvers igjennend Hovedet.' Kjöbenhavn, 1864. Saerskilt Aftryk af Oversigt over d. K. D. Vid. Selsk. Forhandl. i Nov. 1863.

"Observations sur le Développement des Pleuronectes." Par M. Steenstrup. (Annales des Sciences Naturelles, Novembre 1864.)

upon one side as upon a ventral surface, swimming by the undulation of the horizontal unpaired fins.

A new system of equilibrium is established for the Flounders, in which the dorsal and ventral instead of the lateral halves become symmetrical in outline and are equipoised. In most of the Pleuronectidæ, *e. g.* in *Platessa*, *Hippoglossus*, and *Solea*, the left side is the blind side; but in some groups, *e. g. Rhombus* and the young forms termed provisionally *Plagusiæ*, the right side is blind, and the left side bears the eyes. In both of these groups, however, there occasionally occur "wrong Flounders"—dextral Flounders in the sinistral group, and *vice versâ*.

Besides "right" and "wrong" Flounders, we have in each group "double Flounders," individuals in which both sides are nearly equally developed and coloured. These have the eyes placed, one in its ordinary position on the eye-side, and one on the top of the head. They approach the ordinary fish-form, and swim vertically; nevertheless they must be regarded as monsters among the Pleuronectidæ.

The external obliquity of the Flounders is accompanied by important structural deviations. The muscular system of the blind side is much more feebly developed than that of the eye side. The fins are smaller, and, even in the unpaired fins, the lower halves of the fin-rays are weaker. The gills and gill-covers are smaller, and the skin is usually less fully developed. The anterior portion of the face is twisted round, so that the whole mouth is bent towards the blind side, while at the same time the posterior part of the face, in which the eyes are placed, is strongly pressed over to the eye side. There is added to this a remarkable removal of certain portions of the most central part of the face; and this it is which, in connexion with the twisting just mentioned, ultimately brings the eyes into their normal position for each species—both on the same side of the head. This latter condition is universal among Flounders, and may be regarded as essentially characteristic of this curious group.

II.

To understand this clearly, we must determine accurately the position of the eyes of a Flounder with reference to the surrounding parts. The two eyes are not placed in a straight line one above the other: the upper eye is either somewhat behind or somewhat before the lower—usually behind; before in the Soles and the Plagusiæ. The eyes are in opposite positions; their upper margins are turned towards one another, and the lower margin of the upper eye is turned upwards towards the dorsal line of the fish. Between the eyes there stretches a firm bony partition (Mellembalk) formed of definite cranial bones. In the

bony cranium there is a single orbit, entirely surrounded by bone, containing the upper eye only; the lower eye lies outside the orbit, and is protected above by the bones which form its lower margin. These bones are always found to be the frontals and prefrontals belonging to the eye side; and as the lower eye lies under these, it is evident that it is in the usual position with reference to the forehead of its own side. The upper eye, which from its position may be regarded as having belonged to the blind side, and which will be shown to have been seated on the blind side at an earlier stage, lies within the orbit, whose lower border consists of the above-mentioned "partition;" its upper margin is composed of the frontal and prefrontal bones of the blind side. "From this it directly follows that the eye of the blind side has come round to the (inner) side of the frontal bones of the blind side, which is turned towards the middle line, instead of lying at the outer (now upturned) side."

The partition between the eyes, instead of being formed equally from the right and left frontals and prefrontals, is formed only by those of the eye side, right or left, or at most with the addition of a small plate from the frontal bone of the blind side; whilst the remainder of the bone-mass formed by the frontal and prefrontal of the blind side surrounds the lower or upturned margin of the eye, forming the margin of the orbit next the dorsal line. "There is thus an unmistakeable encompassing of the parts, which apparently goes beyond all rule—nay, even beyond all analogy; for usually when parts with definite relations to one another change place, forwards or backwards, upwards or downwards, inwards or outwards, in an organism, the associated parts are moved more or less in the same direction, so that the relative position of the parts remains in the main unchanged." To this rule the different relations which the upper eye in the Flounder bears to its frontal bones forms an exception, which can only be accounted for by a moving round of the parts upon one another. The hitherto received explanation, that the abnormal position of the Flounder's eyes is due simply to a greater or less degree of torsion of the whole head upon the axis of the body, or of a part of the head upon the axis of the head, must therefore be regarded as insufficient, since this position could not have been attained without an actual removal of parts of the head. In many forms the eyes lie close to one another, and the partition between them is quite narrow; while in others the partition is even twice as broad as the diameter of the eye. Sometimes the upper eye lies before the lower, and sometimes behind it—in some cases so far behind it as to seem to rest on the back of the head or the nape of the neck. Notwithstanding all these varieties in position, the relations of the upper eye to the

surrounding bones of the head remain the same in all forms: in all the orbit is excavated in the middle of the forehead, so that the frontal and prefrontal bones of the two sides enclose the eye between them, either immediately between them (as in most Flounders) or so that a narrow plate of the frontal of the blind side helps that of the eye side to circumscribe it beneath (as in the Turbots, Soles, &c.).

A careful analysis of the head in the various groups of Flounders shows that a considerable displacement of associated parts has taken place in a definite direction, the displaced parts still maintaining their original relations in position to one another; the position of the upper eye in relation to its frontal bones (the bones of the blind side) is, however, quite an abnormal one, and cannot be explained by such a displacement or torsion in association with the surrounding parts. Under the generally admitted and correct supposition that the Flounders are not only originally symmetrical, but that they retain this character, and have an eye on each side of the head, for some time after exclusion from the egg, "it becomes necessary to admit that the eye of the blind side, from its original position at that side of the head, has undertaken a movement, deeper and deeper in, under the half-roof which the frontal bone of this side formed over it, and has been brought up through its vault; so that, in order to find room for itself, it has partly separated the frontal bones from one another, partly made its way through the mass of the frontal bone itself." In other words, the eye could not possibly have reached its final position without having passed obliquely in, and up through the head, and come out at the other side. As the nerves and muscles of the eye directly connect it with the bottom of the orbit, the eye must have first passed under the frontal bones, and then up through them. Were we to attempt to explain the new position of the eye by torsion only, the nerves and muscles must have passed over the frontal bones of the blind side, and must lie permanently in that position, which is not the case. The eye, in leaving its original site, however, has attempted to carry the frontal bone of its own side along with it; but the greater part of this bone-mass has resisted, and has remained in its place. The Flounder has thus acquired a firm bony bridge extending from the snout to the back of the head and the vertebral column, and of the utmost importance in connexion with its new condition of equipoise.

III.

The passage of the eye obliquely up through the head is finally proved by direct observations on young Flounders. Mi-

nute pellucid Flounders have been described from the Mediterranean by Rafinesque (under the name of *Bothus diaphanus*, Raf.), and by Risso (*Rhombus candidissimus*, Risso). During the last few years the University Museum of Copenhagen has received several specimens from various parts of the Atlantic, chiefly through two invaluable assistants whom Professor Steenstrup has enlisted in his service in the pursuit of knowledge, Captains Hygom and Andréa, to the former of whom the present memoir is appropriately dedicated. The Atlantic Plagusiæ are about an inch long, and resemble the Mediterranean forms in having the eyes on the left side, and the unpaired fins passing on to the borders of the cheeks; but the upper eye is rather in advance of the lower, and the dorsal and abdominal unpaired fins form with the tail a continuous fringe round the posterior portion of the body. (Pl. XVIII. fig. 2 *C*, *C'*, left and right.) Along with these little Flounders some other small fishes were procured (fig. 2 *A*, *A'*) resembling them in all particulars save in this—that they were apparently quite symmetrical, with an eye on each side of the head. These fishes are Flounders in an earlier stage. Fig. 2 *B*, *B'* represents another form, taken along with them. At *B'* we have the right side of the head, with an eye in the normal place; at *B* we have the left side, with, strange to say, two eyes in the ordinary position of the eyes of a Flounder. On careful examination, however, we find that the eye on the right side is, as it were, pressed inwards into the head, that a new opening surrounded by a thickened border has been prepared for it on the left side, and that it is just on the point of *breaking through* in the new position, being still partly visible from both sides. If we hold the fish in a suitable position with reference to the light, we may even trace an oblique passage up through the head for the transit of the eye, through which the light passes more strongly than through the surrounding parts. A close examination of the stage figured 2 *A* shows us that it is not quite so symmetrical as it appeared at first sight, but that it has already undertaken many of the preliminaries towards the future Flounder form. The mouth is oblique, and the eyes are not seated at the same height, the left being lower than the right. The sides are not equally developed; and from the right eye an oblique, more transparent path may be detected over to the opposite side, up towards a point which corresponds with the subsequent position of the eye.

"More beautiful transitional steps from the symmetrical to the oblique form than those represented in fig. 2 *A*, *B*, *C* could not be given, nor more expressive evidence that the eye actually goes from one side up through the head over to the other side —in other words, that the symmetrical fish by degrees squints

its eye in and up through the head, out to the other side, and at last squints itself into a perfect Flounder."

The other specimens in the museum correspond with the stage fig. 2 *A*, but are not so far advanced. They have characters which indicate that they belong to several species and even genera. It seems, in fact, that at least a whole group of Pleuronectidæ pass through similar early stages; and, from the structure of the mature skulls, it is more than likely that this method of the production of the obliquity of the eyes is universal in the family.

IV.

The author analyses two direct observations which have usually been supposed to support the view that the eyes acquire their final position, both on one side of the head, by a simple torsion of the anterior portion of the head in the young fish. The first of these was made by Professor Van Beneden, and was published by him in the 'Bulletin de l'Académie Royale de Belgique,' t. xx. 1853 ("Note sur la Symétrie des Poissons Pleuronectes dans leur jeune âge").

An extremely minute fish, apparently only recently extruded from the egg, was taken in a fine-meshed net along with Shrimps. The eyes were unsymmetrical—one in its ordinary position, the other higher up, on the top of the head; the dorsal fin came down on the back of the head, but not to the eye; and Van Beneden concludes that a further twist would have brought the eye further down, and that the dorsal fin would then have extended past it over the head.

Prof. Steenstrup gives good reasons for doubting that this very young form was a Flounder at all, and is rather inclined to refer it to *Gunellus*, or some other of the Blenny group. At all events, admitting that it was a Pleuronectid, there is nothing in its structure by any means conclusive against the eye having been ready to perform its migration according to Prof. Steenstrup's view, at a later stage.

The second observation is by A. Malm, Curator of the Göteborg Museum, published shortly after, and independently of, Van Beneden's paper ("Öfversigter Kgl. Sv. Vetenskaps Academien, 1854"). A young *Rhombus barbatus* (Clocq.), 20 millim. long, was found swimming obliquely near the surface of the water. Its colour was nearly the same on both sides; the lower eye was in its usual place, but the upper eye was on the top of the head. The dorsal fin ceased immediately behind the eye.

Malm assumes, 1st, that he had before him an ordinary stage in the development of the species towards its normal form; 2ndly, that the right eye had reached its position at the top of

the head by a simple torsion of the head on its axis; and 3rdly, that, after the passage of the eye down upon the left side by a further torsion, the dorsal fin would have continued its progress over the head. So far as this observation goes, these are mere assumptions, according to Professor Steenstrup's view extremely improbable; but all the structural peculiarities of Malm's fish are most simply explicable if we suppose the young of a "double" *Rhombus* to have fallen into his hands.

This peculiar malformation is by no means uncommon among Flounders. Its main characters are that both sides are coloured and nearly equally developed, that the eye of the blind side is placed in the middle line at the top of the head, while the eye of the eye side is in its normal position, and that the dorsal fin is arrested immediately behind the upper eye, and sometimes somewhat arched over it.

Donovan gives the first figure of this monstrosity, under the name of *Pleuronectes Cyclops*: he imagined it to be a permanent species. His specimen seems to have been a monstrous Brill. Schleep, in the 'Isis' for 1829, describes two "double" individuals of *Rhombus maximus*, and states that he had met with others. Several "double" Flounders are described from the British coast (Yarrell, Couch, &c.). Among the Plaice, the same monstrosity is cited by Malm and Nilsson in *P. Flesus*, and by Kröyer in *P. vulgaris*. Even in the Soles the same peculiarity seems to be indicated by Yarrell in his notice of *Solea Trevelyana*. The Holibut (*Hippoglossus vulgaris*) seems to be the only common form in which a double variety is not described.

It may seem strange that the single individual taken by Malm should have presented this somewhat unusual modification; we must remember, however, that while the common herd of "right" and "wrong" Flounders move along the bottom, "double" Flounders come to the surface, and within range of a towing-net.

V.

Besides the two marked deviations in form from the normal type of each species ("wrong" Flounders and "double" Flounders), there are likewise deviations in colour—"albinos" and "negros." Albinos, white on both sides, but yet normal in form, are mentioned by many authors: by Kröyer in *Platessa vulgaris* and in *P. Flesus* (quoted from Gottsche); by Schleep in *P. vulgaris*: in this latter case no sexual parts could be detected. Houttuyn describes an albino; and Shaw's *Pleuronectes roseus*, from the Thames, belongs to the same category. Flounders dark on both sides, without any structural malformation (negros), seem also to occur, but more doubtfully. They are mentioned

without reference to any malformation; but a more or less perfect "Cyclopean" position of the eye is so often associated with darkness and plumpness on both sides, that there is every reason to believe there is an essential connexion between the two peculiarities. "Double flounders" have always been held in high estimation for the table. The dark side of a Flounder is always the richer; therefore two dark sides are better than a dark and a light: but the advantage seems to go even further; for both sides of a double Flounder are plumper than the best side in the ordinary type. "Wrong Flounders" are met with in all species, but usually rarely. In *Platessa Flesus* they are so common that they can scarcely be regarded as deviations from the normal form: "wrongness" seems in no way connected with structural deviation.

A singular instance exists of a double monstrosity (so far as we know) universal in a species.

Fabricius first describes *Hippoglossus pinguis* (Pl. XVIII. fig. 3), the "Kalleragleck" of Greenland, a small Holibut very abundant and constantly fished in the deepest of the Greenland fiords, sometimes associated with *H. vulgaris* (fig. 4), but often met with alone and in great quantity, with both sides plump and symmetrical, and the eye in the middle of the head. There seem to be good reasons, from the difference in the form of the teeth, from the differences in the gill-covers and in the distribution of the lateral lines, to believe that *H. pinguis* is not to be regarded as the double monstrosity of *H. vulgaris*.

If this be the case, the "right" form of *H. pinguis* has not yet been observed, and we know the species only from its "double" monsters. We are still ignorant of the conditions of reproduction of *H. pinguis*, which has not yet been described as having either roe or milt.

In the paper of which the above is an abstract the distinguished author has clearly made out his principal and most interesting point—that a simple torsion of the anterior portion of the head of a Flounder on its axis is insufficient to explain the final position of the eyes; and his direct observations on the "Plagusiæ" prove that the eye of the blind side actually passes from its own side of the head to the other side—at all events, under the integument and under the subcutaneous tissues which contain the rudiments of the dermal bones forming the support of the anterior border of the dorsal fin, if not actually through the head itself.

The conclusion specially insisted upon by Prof. Steenstrup in the first parts of his communication—that the eye of the blind side, in crossing to the eye side, passes under the frontal bone,

and thus actually through the vault of the cranium—is certainly very remarkable, and, as the author admits, apparently beyond all rule and analogy. We must therefore test carefully the facts which are cited in its support.

Two questions naturally arise:—first, Does the eye of the blind side in the mature skull actually rest in an abnormal position with reference to its essentially associated bones? and secondly, At the period when the migration of the eye took place, were the bones in such a position with relation to the eye as to necessitate its reaching its final position by so unusual a course? We agree with Prof. Steenstrup that the position of the eyes in relation to their associated bones is essentially the same in all the oblique heads of the Pleuronectidæ. We shall select the head of the Turbot (*Rhombus maximus*), a left-handed Flounder, as an example. Placing the head on its side (Pl. XVIII. fig. 1), in its normal position in the living fish, two strong bony beams connect the snout with the middle of the head; and between these, as Prof. Steenstrup describes, lies the large round closed orbit of the right eye. The left beam, which forms the partition between the eyes, is made up principally of the thickened, contracted anterior half of the left frontal bone (fig. 1 *f'*). This is, however, lined throughout its entire length by a strong sickle-shaped process of the right frontal bone, and this process actually forms the left border of the orbit (fig. 1 *f*). Anteriorly and externally the partition is strengthened for about one-third of its length by an articulating process of the left prefrontal (fig. 1 *a'*). The right beam, forming the right border of the orbit, consists almost entirely of the right prefrontal (fig. 1 *a*) enormously developed and synchondrosed with two strong ridges of the right frontal, which, however, in this species, scarcely project in advance of the posterior edge of the orbit. In the Plaice (*Platessa vulgaris*) they advance a considerable distance to meet the opposing process of the prefrontal. The left eye is in its ordinary place beneath the outer edge of the left frontal, the left prefrontal (as usual) merely eking out the anterior extremity of the upper edge of its orbit.

So far as its right frontal is concerned, the right eye is likewise in its normal position, at the outer edge of the sickle-shaped process to which the anterior portion of the right frontal has been reduced.

So far the relations of the eyes to their associated bones has not been disturbed, though an extraordinary shifting and absorption has taken place, which has removed nearly the whole of the right half of the anterior portion of the right frontal bone from the path of the right eye into its new position, and reduced it to a thin crescentic plate.

But the right eye is in a closed orbit whose right border consists of the right prefrontal; and we must account for the position of the eye within this bone, if possible, without resorting to the extreme view that it passed through beneath it. It must always be remembered that the prefrontal bone has no definite relation in position to the eye, whose capsule is essentially connected with the bones of the frontal arch of the skull only. The prefrontal is an extremely variable bone of the face, in relation with the olfactory sense-capsule, if with any. Prof. Steenstrup's diagrams of the path of the eye from the blind to the eye side beneath the cranial bones are all taken from mature distorted skulls; but at the time of the transit of the eye the fish was symmetrical, or nearly so. The eyes were nearly symmetrical; and it would be only natural to conclude that the bones of the head (or their potential positions) were nearly symmetrical likewise. The left border of the skull remains normal throughout, the parts occupying nearly the same relative positions which they do in the Cod; *i. e.*, the left eye is opposite the lower edge of its own frontal bone, the comparatively small prefrontal merely finishing the anterior edge of its orbit. It is clear that the left eye of the Turbot or either of the eyes of the Cod might migrate across the head under the skin, merely absorbing or pressing before it the frontal bone, without coming in contact with the prefrontal at all. In the Turbot the left prefrontal is nearly normal in size, and not more than half the length of that of the right side; and I think we may conclude that in the symmetrical young both bones were normal and alike, and that the right eye was placed opposite the edge of the frontal bone, which at that time formed a portion of the right edge of the skull. When the change in the position of the eye occurred, this exposed portion of the right frontal, whether potential or actually developed, was pushed or absorbed before the migrating eye and its nervous and muscular connexions, and reduced to the crescentic plate which, in the mature head, lines the left wall of the orbit, still retaining its original position with reference to the eye. At a subsequent stage in the development of the oblique head, the right prefrontal shot out a process backwards across the gap through which the nerves and muscles of the eye had passed, and became articulated to the frontal bone, forming the beam whose immediate relation to the new condition of equilibrium—that is to say, to the obliquity of the fish—is so accurately pointed out by Prof. Steenstrup.

From these considerations we are forced to conclude that the eye of the blind side passed to the eye side, not through the vault of the head, but under its integument, displacing in its progress the frontal bone of its own side—the space through

which its nervous and vascular connexions passed being indicated in the mature skull by the unsymmetrical posterior half of the articulating process of the right prefrontal, the eye having maintained its normal relation to its associated bone (the right frontal) throughout.

The term "migration" of the eye is, of course, used in a somewhat metaphorical sense. The eye changes little in *actual* position. With the growth of the fish the associated parts are, as it were, *developed past it*, producing this singular obliquity.

Nothing can be more startling than the effect produced by the changes in the position of the eye in these young Flounders. We were kindly introduced last summer to the charming little "Plagusiæ" by Prof. Steenstrup in his most instructive museum. At first symmetrical miniature "jaunes-dorées;" next the right eye becoming depressed inwards, and a strange little button-hole appearing opposite it on the eye side, giving singularly the effect of a Flounder with three eyes; the eye slipping into the button-hole, and finally all trace of its former socket becoming gradually obliterated. Still, notwithstanding the wonderful appearance of this migration, if our view be correct, but little violence is done to the relations of the parts. The eye was always under the skin, and it merely passes in its course beneath a band of opake integument to emerge under a second "pane" of transparent skin which has been prepared for its reception.

A valuable lesson may be drawn from Prof. Steenstrup's most interesting observations upon "right" and "wrong" Flounders, "double" Flounders, "albinos," and "negros." The dark side of a Turbot is infinitely the more fully developed, the richer, the fatter, the better in every way. According to modern usage, if a Turbot be put on the table, this eye side is turned downwards; and the consequence is that usually, after the thin, meagre blind side has been discussed in the dining-room, most of the best of the fish is sent down to the servants' hall. It may not be the cook's interest to remedy this, but surely it is her mistress's; for, under the present system, no *lady*, at all events, can hope to reach the eye side of a Turbot.

EXPLANATION OF PLATE XVIII.

Fig. 1. Skull of the Turbot (*Rhombus maximus*): *a*, right prefrontal; *a'*, left prefrontal; *f*, right frontal; *f'*, left frontal.

Fig. 2. Heads of *Plagusiæ* (left and right sides) in three stages of metamorphosis.

Fig. 3. *Hippoglossus pinguis* (Fabr.).

Fig. 4. *Hippoglossus vulgaris* (Flem.).